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ON THE INTERPRETATION OF CERTAIN TROPISMS OF INSECTS¹

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THE great interest which has developed among zoologists during recent years regarding the behavior of animals has resulted in such a large number of papers on tropisms and related topics, that a short discussion of the matter in regard to insects may seem rather uncalled for at present.

The field of entomological research affords, however, so many possibilities in this line that the activity which was formerly confined to studies of lower invertebrates is gradually showing a tendency to shift or to widen out toward the insects in its search for fresh subjects, and already the reactions of various species belonging to several groups have been investigated by the commonly accepted methods. The problem of studying the responses of insects to light, gravity, mechanical stimuli, etc., involves so many factors which do not enter into any consideration of simple organisms like protozoa or planarians that its complexity is rarely appreciated by those who give it their attention. The former animals can be brought into the laboratory and placed where the normal conditions of their natural environment are reproduced more or less faithfully. Under such circumstances their reactions and behavior can be analyzed by means of different mechanical contrivances which have been devised to test the influence of certain stimuli to the exclusion of others. To be brief, experience has shown that conclusions derived from such experiments are fairly trustworthy, and that a close approach can be thus made

¹ A paper read before the joint meeting of the Wisconsin Academy of Sciences, Arts and Letters and the Wisconsin Natural History Society at Milwaukee, February 13, 1908.

to an understanding of the animals' behavior in their natural environment. The extension of these methods into the study of such highly specialized and delicately organized invertebrates as insects is fraught by many dangers, and the failure to recognize certain inherent difficulties must inevitably invalidate some of the general conclusions which have been recently announced.

Without reference to the psychological aspect of insect behavior which I am in no way competent to consider, there are a number of factors entering into the study of reactions which I believe must be recognized if we are to appreciate the fundamental difference between a natural environment and an artificial reproduction of its single features in the laboratory.

Probably more experiments on insects have been recorded which bear upon the phenomena of phototropism than upon any other single tropism, and we may therefore reasonably suppose that the results in this field represent actual conditions as well as, if not better than, those on other tropisms.

Turning to a recent paper by Frederick W. Carpenter on the reactions of the pomace-fly, *Drosophila ampelophila*, to various stimuli,² we see the statement:

"Light has both a kinetic and directive effect. The insect moves toward the source of light, being positively phototropic. The directive effect is apparent only when the kinetic stimulus is sufficient to induce locomotion."

This is merely a concise expression of the fact which we have all observed many times of the fly buzzing on the window. Under such conditions most Diptera are positively phototropic and will go through long series of alternating periods of activity and quiescence, the former usually induced by some external stimulus; attempting all the while to pass through the window toward the source of illumination. With many species this may often continue until the death of the insect from exhaustion and lack of food.

² AMERICAN NATURALIST, vol. 39, pp. 157-171, 1905.

Such are the results of experimentation where the transparent sheet of glass has been allowed to change the normal conditions of environment. Let us suppose, however, that the fly be allowed to pass out of the window into a more nearly natural environment. It immediately flies into the open, but does not endeavor for any length of time to continue its positively phototropic movements. Once unrestrained it is soon again following the normal pursuits of its particular species, which in the case of the aforementioned *Drosophila* is principally to locate decaying vegetable matter which will be suitable for food, breeding, and oviposition. It is evident in this case that the universal and quick response of the *Drosophila* to light when confined is due to some added factor in the experiment which I hope to point out on a later page.

Another paragraph in the same paper refers to results obtained under still more unnatural conditions.

“The exposure of *Drosophila* to light of high intensity is accompanied by an increase in the kinetic effect. Under the influence of the highest intensity used, that of a 250 c.p. arc light at 40 cm., the muscle reflexes of an insect become very rapid and violent, and the directive influence of the light seems inhibited.”

When we realize that these insects are as quick as ourselves to appreciate sudden changes in light and shade at short distances, it is not astonishing that they are unable to orient themselves under such startlingly unnatural conditions, placed only sixteen inches from an arc light, and their behavior here can not be compared with their reactions to normal daylight or sunlight. In fact the perversion of instinct induced by electric arc lights is a common experience with many nocturnal insects which are attracted in countless numbers, while their normally phototropic diurnal relatives are disturbed scarcely at all by the presence of the lights.

This too, is a matter of common experience, which has found expression in the adage of the moth and the flame. Most of the *Lepidoptera heterocera* are negatively phototropic, venturing out at dark and concealing themselves

from the light during the day, yet the proximity of an unnaturally brilliant light quickly upsets their normal instincts, and they are irresistibly attracted, although the appearance of the moon or the dawn affects them in no such manner.

Another tropism which is easily investigated by experimental observation is geotropism, and the agreement reached by a number of workers is that many insects when confined in an unnatural environment are negatively geotropic. To quote again from the same paper on *Drosophila*:

“Gravity has a directive effect upon the active insect which is negatively geotropic, that is, the insect moves away from the center of the earth.”

Such is indeed the action of almost any insect, particularly an active species or a flying one when placed in any sort of a receptacle where it is deprived of food, or where it can not enjoy the freedom to which it is accustomed. It immediately flies or crawls upward, and usually will repeat the process almost indefinitely if for any reason it finds itself again at the bottom. Since it always goes to the top of the jar if not attracted in another direction by other stimuli, negative geotropism is taken to be one of its normal attributes.

This negative geotropism, however, becomes an absurdity as soon as we attempt to apply it in a general way to insects in their natural environment. Crawling insects do not congregate at the tops of objects in their environment, and neither do flying insects approach high altitudes, far from the surface of the earth. After their first escape from unnatural restraint, their negative geotropism vanishes as quickly as did their positive phototropism. The effect of any sudden and unnatural disturbance on the action of a flying insect is very easy of observation and is experimentally tested many hundreds of times during a season by any active collector of insects. Take, for example, a common bumblebee, which on account of its large size can be easily followed by the eye

as it passes from flower to flower, often traversing a considerable space in a nearly straight line toward a particular plant whose location may be known to it through past experience. Thus it continues along, sometimes rising slightly or flying lower, but exhibiting no movements whatever which could be attributed to geotropism or phototropism.

Let it be caught in the collector's net, however, and it immediately develops the negative geotropism, flying wildly about and seeking to ascend. If the net be kept inverted it will not escape until it accidentally drops out as a result of flying at the cloth of the net or of losing its foothold in crawling upward. Once out, it soars upward perhaps a short distance, and then resumes its former occupation.

Do these actions of the fly and the bee when confined, which are characteristic of other insects as well, represent their normal tropisms?

It has been usually assumed that they do, and several ingenious explanations have been suggested which endeavor to show why phototropism and negative geotropism become inactive in nature after certain periods, since the logical result of their continued action never presents itself to observation.

From the behavior of species in nature, these are most certainly not normal and are evidently caused by the conditions of the experiment. The most probable explanation of their appearance is that they are the expression of an instinct to seek the open whenever disturbed. In nature this freedom can always be obtained by flying upward and toward the light, that is to say, by phototropic and negatively geotropic movement which carries them away from all obstacles. Such a reflex in response to disturbances is a very valuable one and is no doubt maintained by natural selection, since it automatically offers an avenue of escape from disturbing conditions or danger.

In some species this reflex is in another direction, and these exceptions are most instructive in support of this

idea. Bees of the parasitic genus *Cœlixys* when caught in the net almost invariably fly downward at the first impulse, being thus positively instead of negatively geotropic. A reason for this adaptation can be suggested from a knowledge of their habits. Graenicher³ has recently shown that *Cœlixys* enters the nests of other bees to lay its eggs. Thus in the event of its discovery by the rightful owner of the nest, it may drop to the ground with much better chances for escape than it would otherwise have.

Tiger beetles of the genus *Cicindela* are active fliers, but are more at home on the ground, consequently when covered by the net they never rise on the wing, but invariably attempt to escape on the surface of the ground, which they can readily do if the net does not fit very closely. Their actions can thus be traced directly to an adaptation.

From any unbiased review of such facts, I think it will appear that we can not hope to make wholly satisfactory progress along the line of interpreting insect behavior by means of studying their responses to stimuli in the laboratory, unless this be done with careful reference to their habits and behavior in nature, and in relation to the various external factors of their environment.

³ *Bull. Wisconsin Nat. Hist. Soc.*, vol. 3, p. 162, 1905.